

EFFECTS OF WEATHER ON PARROT GEOPHAGY IN TAMBOPATA, PERU

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ABSTRACT.—Geophagy is widespread and well documented for mammals, but avian geophagy has only recently become the subject of serious scientific investigation. I analyzed data from 606 mornings of observations at a large avian geophagy site or “clay lick” in the southwestern Amazon Basin to examine the effects of weather on bird lick use. Birds used the clay lick on 94% of the mornings without precipitation or fog. Parrots dominated the site in both numbers of species (17) and individuals (>99%). Weather conditions were significantly correlated with total lick use: there was greater use on sunny mornings and less on rainy mornings. Fog and overnight rain were correlated with low lick use. Sun, rain, fog, and overnight rain were recorded on 47, 25, 20, and 8% of the mornings, respectively. I estimated that inclement weather caused an annual 29% reduction in geophagy for all bird species combined. When early morning rain prevented species from using the lick, they did not return later in the day nor did they compensate for rainy mornings by increasing lick use on subsequent days. The timing of lick use and the lack of compensation suggest that neutralization of toxins could be driving lick use in this system. *Received 25 August 2003, accepted 26 May 2004.*

Geophagy, the intentional consumption of soil, is widespread among vertebrate and invertebrate taxa including mammals, birds, reptiles, and insects (Sokol 1971, Arms et al. 1974, Davies and Baillie 1988, Benkman 1992, Smedley and Eisner 1996). Geophagy occurs on all continents (except Antarctica) and is particularly well documented for mammals, including humans and other primates (Jones and Hanson 1985, Abrahams and Parsons 1996, Klaus and Schmidt 1998, Wiley and Katz 1998, Krishnamani and Mahaney 2000). Recent studies of avian geophagy in tropical areas have focused on soil chemistry, physiology, or short-term observations of behavior (Diamond et al. 1999, Gilardi et al. 1999, Burger and Gochfeld 2003, Brightsmith and Aramburú in press). Long-term studies of geophagy sites are lacking and this hinders our ability to understand the ecological role and relative importance of this phenomenon. Here, I document the effects of weather on avian geophagy in a lowland tropical forest over a 3-year period.

Geophagy is known for members of the avian orders Anseriformes, Columbiformes, Passeriformes, Casuariiformes, Galliformes, and Psittaciformes (Jones and Hanson 1985, Benkman 1992, Wink et al. 1993, Diamond et al. 1999, Keppie and Braun 2000). Of these, the most conspicuous and well studied are the

parrots (Psittaciformes), which gather by the hundreds to consume clay-rich soils from riverbank sites in South America (Emmons and Stark 1979, Gilardi et al. 1999, Burger and Gochfeld 2003, Brightsmith and Aramburú in press). The soils from these “clay licks” apparently provide an important source of sodium and protection against dietary toxins (Diamond et al. 1999, Gilardi et al. 1999, Brightsmith and Aramburú in press). These soils likely permit geophagous species to exploit a wider range of plant resources and allow the high diversity and density of parrots found in the western Amazon basin (Diamond et al. 1999). However, geophagy is not practiced by all psittacids. This variation in geophagous behavior within locations over time and between locations provides an opportunity to explore the ecological role of geophagy.

Weather is known to have strong effects on bird survival and behavior (Silleet et al. 2000, Takagi 2001, Winkler et al. 2002, Cougill and Marsden 2004). Rain and lower temperatures cause short-term increases in nutritional stress for birds and often reduce the frequency of behaviors not critical to immediate survival, including song, migration, communal roosting, and flying (Pyle et al. 1993, Keast 1994, Lengagne and Slater 2002, Lopez-Calleja and Bozinovic 2003, Cougill and Marsden 2004). However, rain and lower temperatures often cause an increase in foraging, a behavior needed for short-term survival (Finney et al. 1999, Fischer and Griffin 2000, Dewasmes et

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al. 2001). I hypothesized that inclement weather (rain and fog) would decrease lick use and that birds would compensate for this decrease by using the lick more after the weather cleared.

METHODS

Study area.—I studied avian geophagy at a clay lick near the Tambopata Research Center (13° 08' S, 69° 37' W) in southeastern Peru. The center is on the border of the Tambopata National Reserve (275,000 ha) and the Bahuaia-Sonene National Park (537,000 ha) in the department of Madre de Dios. The center lies at the boundary between tropical moist and subtropical wet forest at an elevation of 250 m and receives 3,200 mm of rain per year (Tosi 1960; this paper). The research center is located in a small (<1 ha) clearing surrounded by mature floodplain forest, successional floodplain forest, *Mauritia flexuosa* (Arecaceae) palm swamp, and upland forest (Foster et al. 1994). A large patch of bamboo (*Guadua sarcocarpa*; Poaceae) covered the area immediately adjacent to the clay lick, but this patch flowered and died in 2001–2002 (Foster et al. 1994, Griscom and Ashton 2003, DJB pers. obs.). The clay lick is a 500-m long, 25- to 30-m high bank along the western edge of the upper Tambopata River, approximately 300 m from the research center. The cliff is formed by the Tambopata River's erosion of uplifted, Tertiary-age alluvial sediments (Räsänen and Salo 1990, Foster et al. 1994, Räsänen and Linna 1995). The soils of the lick are rich in clay with high cation exchange capacity and high sodium levels (Gilardi et al. 1999, DJB unpubl. data).

Weather data.—From June 1995 through February 2003, researchers at the site recorded weather data. Daily maximum and minimum temperatures were taken from a mercury max-min thermometer located in the understory of primary floodplain forest approximately 20 m from the forest edge. Rain data were collected using a standard rain gauge in a clearing approximately 30 m from the forest edge. Observers recorded the approximate time of rainfall on all days, even when not observing the clay lick. We did not collect weather data every day and gaps of 1 day to >1 month occurred. I calculated mean rainfall for all months in which there were no gaps in

the data >2 days (63 of 93 months). The mean rainfall for each month of each year was used to calculate the overall monthly mean and standard deviation (e.g., the data from January of each year was averaged to provide a composite rainfall for January). Data collected during the El Niño Southern Oscillation of December 1997 to June 1998 were omitted due to the highly irregular patterns of rainfall that typically occur during such events. The average annual rainfall total was calculated by summing the means for each month. Data on the timing and duration, but not intensity of rain, fog, and insolation, were collected during observations of the clay lick (see Bird data below).

Bird data.—Observers recorded bird use at the clay lick on 606 mornings from 12 January 2000 to 16 November 2002. Observers began watching the lick before the birds arrived (approximately at sunrise) until the birds finished their early morning lick use (usually before 07:30 EST). On 280 occasions, observers conducted full-day observations (sunrise until 16:00–17:30), but only early morning data are reported here. Every 5 min, observers recorded the weather as rain (rain falling on the observer), sun (sun hitting the ground anywhere in the vicinity of the clay lick), or cloud (if neither of the others applied). We also noted the presence or absence of fog. Observers recorded the time, number, and species of the first birds that landed on the lick. Starting from this point, observers counted all birds on the lick every 5 min using binoculars and a spotting scope (20–60× zoom). Observers could readily distinguish all of the common bird species on the lick except the two, small, green macaws: Chestnut-fronted Macaw (*Ara severa*) and Red-bellied Macaw (*Orthopsittaca manillata*). For this study, these two species are lumped together and analyzed as “green macaws.”

Data analysis.—I analyzed the correlation between weather variables, month, and lick use using a quasi-likelihood general linear regression (e.g., a Poisson regression with overdispersion; Agresti 2002). This type of model was needed because the birds traveled in flocks and descended to the lick en masse, causing the variance in daily lick use to be greater than the mean. The main effects included in the analysis were year, month,

weather index, rain the night before, fog, daily minimum temperature, daily maximum temperature, lick use the day before, the number of days since the lick was used, and two-way interaction terms. The dependent variable was lick use measured in bird minutes. Bird minutes were defined as the number of birds on the lick multiplied by the number of minutes they stayed on the lick (i.e., 4 birds for 15 min each = 60 bird min). The weather index was a composite variable based on the observations of sun, cloud, and rain recorded every 5 min during observations. It was calculated as the average for each morning with sun = 1, cloud = 2, and rain = 3. Rain the night before was recorded as present if rain fell between 20:00 and 04:00. The variable "fog" used in the model was the sum of the number of 5-min intervals in which fog was recorded during each morning observation. "Lick use the day before" was the number of bird minutes of lick use recorded on the preceding day. The "number of days since the lick was used" was the number of days since birds used the lick. I considered the lick used by birds on a given morning if the total number of bird minutes recorded was >10% of the average for that month. For the calculation of lick use the day before and number of days since the lick was used, I assumed that total lick use was zero for days when heavy rain all morning prevented the observers from going to the lick. This assumption is justified because on 12 mornings, where rain was recorded >80% of the time, total lick use averaged only 39 ± 107 bird min (SD) or 1.3% of the lick use for fair weather days (mean_{fair weather days} = 3051 ± 2465 SD, $n_{fair weather days}$ = 386).

The first regression analysis included all variables. Then I excluded all variables that did not contribute significantly to the model and reran the analysis. Finally, I ran a separate analysis on each of the excluded variables to determine whether any of them contributed significantly to the model (Pyle et al. 1993). The daily maximum temperature was correlated with both the daily minimum temperature (Pearson product-moment correlation = 0.45) and the weather index (Pearson product-moment correlation = -0.35), and it explained less variation than either of the other two, so it was eliminated from the analysis. The interaction coefficient of fog by daily

minimum temperature was highly correlated with the coefficient of fog (Pearson product-moment correlation = 0.998) and the inclusion of the interaction term caused both fog and the interaction to become nonsignificant, so this interaction term was removed from the analysis. This procedure was repeated using lick use for each individual species as the dependent variable. Means are reported \pm SD.

To measure potential lick use, for each month I calculated daily average lick use for each species using data only from "fair weather" mornings (i.e., mornings with no fog, rain, or rain the night before). To measure actual lick use, for each month I calculated daily average lick use for each species using data from all days regardless of weather. For actual lick use, I included mornings with continuous heavy rain when the observers did not go to the lick and assumed that total lick use was zero. The total reduction in lick use due to weather was estimated by the following formula: (potential lick use - actual lick use)/potential lick use.

RESULTS

A total of 28 species of birds ate soil from the lick (Table 1). Parrots dominated the site, both in number of species ($n = 17$) and number of observations (>99%). Thirteen species used the lick regularly in the early mornings (before 07:30) and are included in the analyses presented here. The remaining species were either too uncommon to include in the analysis ($n = 11$) or did not use the lick in the early morning ($n = 4$). Of the 13 species that used the lick in the early morning, 4 also used the lick in the late morning and afternoon (Table 1): Blue-throated Piping-Guan (*Pipile cumanensis*), Blue-and-yellow Macaw (*Ara ararauna*), Scarlet Macaw (*A. macao*), and Red-and-green Macaw (*A. chloroptera*).

Weather.—The average annual rainfall at Tambopata Research Center was 3,236 mm. Monthly mean rainfall ranged from 95 ± 57.7 mm in August ($n = 6$ years) to 528 ± 172.4 mm in January ($n = 7$ years). The months of July and August were the only two in which mean rainfall fell below the estimated potential evapotranspiration (Fig. 1). Rain events of >1 mm were recorded on 42% of the days (709 of 1,679 days). The number of days with rain was greatest in January (mean = $18 \pm$

TABLE 1. Species recorded eating soil from the clay lick at Tambopata Research Center in southeastern Peru, 12 January 2000–16 November 2002. Abundances are given as C (common, seen during $\geq 75\%$ of the observations), U (uncommon, seen $< 75\%$ and $\geq 25\%$), R (rare, seen $< 25\%$ and $\geq 5\%$), or O (occasional, seen during $< 5\%$ of the observations). For species listed as occasional, the number of times seen is reported in parentheses.

	Time of day			Abundance at lick
	Before 07:30	07:30–12:00	After 12:00	
Species analyzed in this paper				
Blue-and-yellow Macaw (<i>Ara ararauna</i>)	x	x	x	C
Scarlet Macaw (<i>Ara macao</i>)	x	x	x	C
Red-and-green Macaw (<i>Ara chloroptera</i>)	x	x	x	C
Chestnut-fronted Macaw (<i>Ara severa</i>)	x			C
Red-bellied Macaw (<i>Orthopsittaca manilata</i>)	x			C
White-bellied Parakeet (<i>Aratinga leucophthalmus</i>)	x			U
Dusky-headed Parakeet (<i>Aratinga weddellii</i>)	x			U
White-bellied Parrot (<i>Pionites leucogaster</i>)	x	x		U
Orange-cheeked Parrot (<i>Pionopsitta barrabandi</i>)	x			U
Blue-headed Parrot (<i>Pionus menstruus</i>)	x			C
Yellow-crowned Parrot (<i>Amazona ochrocephala</i>)	x			U
Mealy Parrot (<i>Amazona farinosa</i>)	x			C
Blue-throated Piping-Guan (<i>Pipile cumanensis</i>)	x	x	x	U
Additional species recorded at the lick				
Speckled Chachalaca (<i>Ortalis guttata</i>)	x	x	x	R
Spix's Guan (<i>Penelope jacquacu</i>)	x	x	x	R
Orange-breasted Falcon (<i>Falco deiroleucus</i>)		x		O (1)
Plumbeous Pigeon (<i>Patagioenas plumbea</i>)		x	x	U
Pale-vented Pigeon (<i>Patagioenas cayennensis</i>)		x	x	U
Ruddy Pigeon (<i>Patagioenas subvinacea</i>)		x	x	U
Blue-headed Macaw (<i>Prinolius coultoni</i>)	x			R
Dusky-billed Parrotlet (<i>Forpus sclateri</i>)		x	x	R
Amazonian Parrotlet (<i>Nannopsittaca dachilleae</i>)		x	x	O (9)
Tui Parakeet (<i>Brotogeris sanctithomae</i>)		x	x	O (1)
Cobalt-winged Parakeet (<i>Brotogeris cyanoptera</i>)		x	x	U
Gray-fronted Dove (<i>Leptotila rufaxilla</i>)		x	x	O (2)
Purplish Jay (<i>Cyanocorax cyanomelas</i>)		x	x	O (4)
Blue-gray Tanager (<i>Thraupis episcopus</i>)		x	x	O (4)
Crested Oropendola (<i>Psarocolius decumanus</i>)	x			O (2)

4.1 days, $n = 7$ years) and least in August (mean = 5.5 ± 2.6 days, $n = 6$ years). The mean temperature was $24.3 \pm 1.4^\circ\text{C}$. Early morning fog was recorded on 20% of the days ($n = 606$). Rain was recorded during 12% of the observations ($n = 606$). It rained the previous night during 8% of the observations ($n = 510$); there was no rain or fog of any sort for 76% of the observations ($n = 510$). On 80 days there was heavy rain during the early morning (and observers did not go to the lick on these days).

Weather effects on geophagy.—Birds used the clay lick on 94% of the fair weather mornings (i.e., without rain or fog during the observation or rain the night before, $n = 386$).

The variables month, weather index, fog, and rain the night before explained 47% ($P < 0.001$) of the variation in total lick use (Table 2). As weather progressed from sunny to cloudy to rainy, and fog duration increased, total lick use decreased, explaining 7% of the variation in the data ($P < 0.001$; Table 2). Birds used the lick less on early mornings following rain the previous night ($P < 0.05$; Table 2). Month explained 39% of the variation in total lick use ($P < 0.001$; Table 2); mean daily lick use ranged from $4,784 \pm 2,387$ bird min in August to 257 ± 378 bird min in May (Fig. 2).

When each taxon was analyzed separately, lick use was negatively correlated with weath-

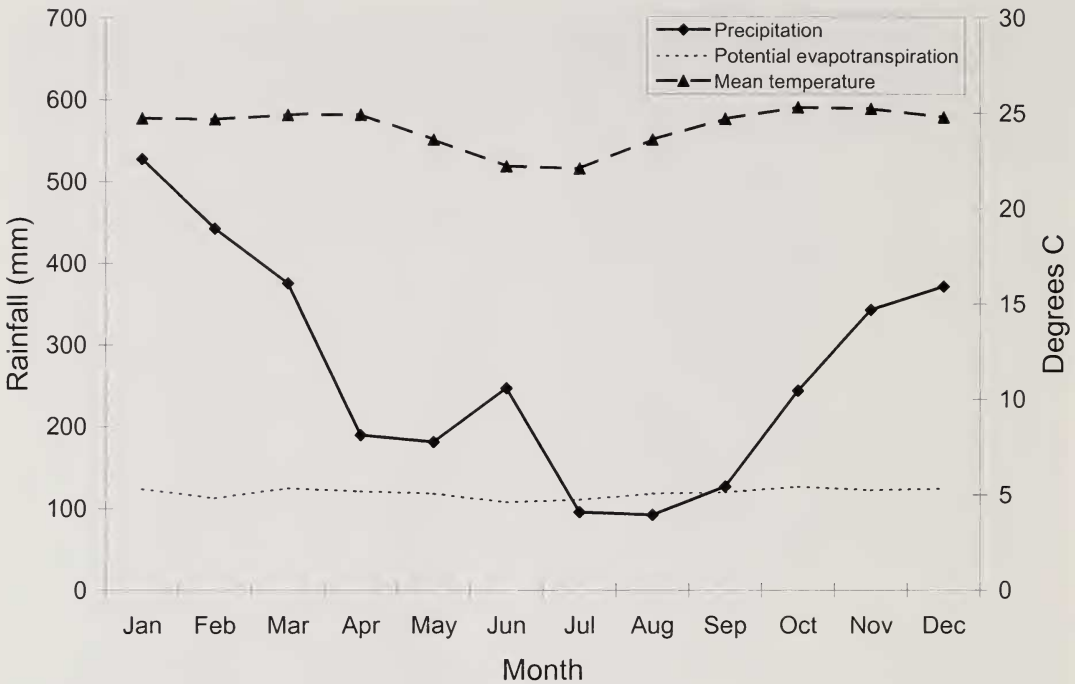


FIG. 1. Mean monthly temperature, rainfall, and estimated evapotranspiration at Tambopata Research Center, Peru, June 1995 through February 2003. Evapotranspiration was estimated following Holdridge (1967).

TABLE 2. Quasi-likelihood general linear regression model (Poisson regression with overdispersion) of weather and month affecting lick use by birds in Tambopata, Peru, 12 January 2000–16 November 2002. Values are presented for combined lick use by 13 species and as the percent deviance explained (regression coefficient). Coefficients with negative values indicate that birds used the lick less as the value of the independent variable increased. A single coefficient cannot be calculated for the categorical variable month, and so is not reported. The model uses the chi-squared-based analysis-of-deviance test. The overall model is significant at $P < 0.001$.

Variable	Deviance (regression coefficient)
Month	39%***a
Weather index	4% (-0.36) ***
Fog	3% (-0.038)***
Rained night before	1% (-0.32)*
Year	NS ^b
Birds yesterday	NS
Days since used ^c	NS
Daily minimum temperature	NS
Month:weather ^d	NS
Month:fog ^d	NS
Daily minimum:weather index ^d	NS
Total df	509
Total deviance	229,190
Deviance explained	47%

a * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

b NS = not significant ($P > 0.05$).

c Days since used is a measure of how many mornings had elapsed since the lick had been used by birds.

d Variables separated by a colon indicate interactions.

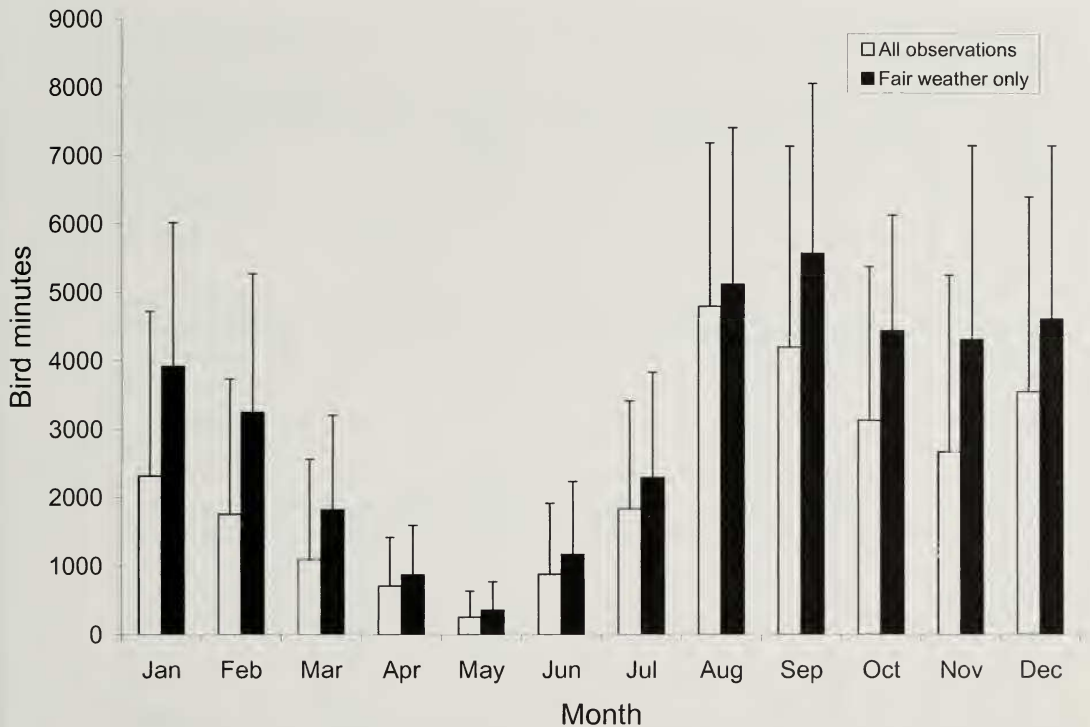


FIG. 2. Mean daily lick use (bird min) by month for all mornings (white bars) and fair weather mornings (black bars) at a clay lick in Tambopata, Peru, 12 January 2000–16 November 2002. Fair weather mornings are defined as those without rain, fog, or rain the night before. Error bars indicate ± 1 SD. The data for fair weather mornings measure potential lick use while data for all days measure actual lick use. The difference between lick use for fair weather mornings and lick use for all mornings is an estimate of the reduction in lick use caused by inclement weather ($n_{\text{fair weather days}} = 307$, $n_{\text{all days}} = 643$).

er index for 7 of 12 taxa analyzed (all $P < 0.05$) indicating that decreased sun and increased rain correlated with reduced lick use (Table 3). Weather index explained 0.4–6.0% of the variation in lick use for these species (Table 3). As fog increased, lick use decreased significantly for 8 of 12 taxa, explaining 0.4–3.0% of the variation in lick use for these species (all $P < 0.05$; Table 3). Four species used the lick less on mornings following overnight rains (all $P < 0.05$; Table 3) while the White-bellied Parrot (*Pionites leucogaster*) used the lick more on mornings following rain ($P < 0.05$). Mealy Parrots (*Amazona farinosa*) showed a positive interaction between weather index and the daily minimum temperature, suggesting that sun and rain had less effect on their lick use during warm days ($P < 0.001$; Table 3). The year-to-year differences were not significant for 8 of 12 species (all $P > 0.05$; Table 3). For the remaining four species

the changes were mixed: Red-and-green and Blue-and-yellow macaws increased with year ($P < 0.001$ and $P < 0.05$, respectively) while Yellow-crowned Parrots (*Amazona ochrocephala*) and White-eyed Parakeets (*Aratinga leucophthalmus*) decreased ($P < 0.05$ both species; Table 3). For Red-and-green Macaw and Orange-cheeked Parrot (*Pionopsitta barabandi*), lick use increased with daily minimum temperature ($P < 0.05$ both species). All species showed a highly significant month effect, indicating strong seasonality in lick use ($P < 0.001$; Table 3). Month explained 17–60% of the variation in the data. For Mealy Parrots, there were significant effects of month by fog and daily minimum temperature by weather index ($P < 0.001$; Table 3).

Lick use on fair weather mornings (a measure of the potential lick use), and lick use on all days, including rainouts (a measure of the actual lick use), showed almost identical

TABLE 3. Quasi-likelihood general linear regression models (Poisson regression with overdispersion) of weather and month on lick use by birds in Tambopata, Peru, 12 January 2000–16 November 2002. Values are presented for 12 taxa representing 13 species that used the clay lick during the early morning (before 07:30). Values are presented as percent deviance explained (regression coefficient). Coefficients with negative values indicate that birds used the lick less as the value of the independent variable increased. Single coefficients cannot be calculated for the categorical variable month or interactions including month, and so are not reported. The model uses the chi-squared-based analysis-of-deviance test. All models are significant at $P < 0.001$.

Variable	Red-and-green Macaw	Blue-and-yellow Macaw	Scarlet Macaw	Green macaws ^f	Mealy Parrot	Yellow-crowned Parrot
Month	23%***	29%***	23%***	17%***	39%***	27%***
Weather index	NS ^b	4% (-0.54)***	6% (-0.60)***	5% (-0.74)***	3% (-5.36)***	NS
Fog	2% (-0.074)**	3% (-0.069)***	3% (-0.056)***	3% (-0.037)***	NS	2% (-0.049)***
Rained night before	NS	1% (-0.60)*	2% (-0.83)**	NS	NS	NS
Year	5% (0.75)***	1% (0.23)*	NS	NS	NS	1% (-0.26)*
Birds yesterday	1% (0.008)*	2% (0.003)**	NS	NS	NS	NS
Days since used ^e	2% (-0.69)**	2% (-0.40)**	NS	NS	NS	NS
Daily minimum temperature	2% (0.17)*	NS	NS	NS	NS	NS
Month:weather index ^d	NS	NS	NS	NS	NS	NS
Month:fog ^d	NS	NS	NS	NS	6%***	NS
Daily min. temp.:weather index ^d	NS	NS	NS	NS	1% (0.21)**	NS
Total df ^e	442	406	509	605	559	605
Total deviance	6,765	21,081	13,579	65,185	145,187	16,140
Deviance explained	35%	42%	32%	25%	48%	30%

Variable	Blue-headed Parrot	Orange-checked Parrot	White-bellied Parrot	White-eyed Parakeet	Dusky-headed Parakeet	Blue-throated Piping-Guan
Month	55%***	59%***	60%***	36%***	27%***	18%***
Weather index	0.4% (-0.14)*	1% (-0.33)**	NS	2% (-0.11)**	NS	NS
Fog	0.4% (-0.022)*	0.5% (-0.030)*	NS	1% (-0.02)**	NS	NS
Rained night before	0.3% (-0.37)*	NS	1% (0.39)*	NS	NS	1% (-1.00)*
Year	NS	NS	NS	6% (-0.26)***	NS	NS
Birds yesterday	NS	NS	1% (0.013)**	11% (0.0018)***	NS	2% (0.037)*
Days since used ^e	NS	NS	1% (-0.40)*	11% (-0.31)*	NS	NS
Daily minimum temperature	NS	1% (0.083)*	NS	NS	NS	NS
Month:weather index ^d	NS	NS	NS	NS	NS	NS
Month:fog ^d	NS	NS	NS	NS	NS	NS
Daily min. temp.:weather index ^d	NS	NS	NS	NS	NS	NS
Total df ^e	509	559	406	477	605	406
Total deviance	120,386	40,211	6,497	67,502	26,217	1,891
Deviance explained	57%	61%	62%	61%	27%	21%

^a $P < 0.05$, ^{**} $P < 0.01$, ^{***} $P < 0.001$.
^b NS = not significant ($P > 0.05$).
^c Days since used is a measure of how many mornings had elapsed since the lick had been used by birds.
^d Variables separated by a colon indicate interactions.
^e Total df vary because different variables had different numbers of observations eliminated due to missing values.
^f The taxon "green macaws" is a combination of Chestnut-fronted and Red-bellied macaws.

month-to-month patterns (Fig. 2). The difference in lick use between fair weather mornings and all mornings combined suggests that inclement weather caused an annual 29% reduction in early morning lick use. Monthly reduction in lick use ranged from 6% in August to 46% in February. Among the 12 taxa analyzed, reduction in lick use ranged from 16 to 37%.

When rain or fog occurred from 05:00 to 07:30 it almost completely prevented the early morning species from using the lick. On 7 of 21 such days, a small number of individuals of the "early morning species" would occasionally use the lick in the late morning or afternoon. However, the number of individuals of early morning species using the lick on these afternoons was always small and total use of the lick averaged <2% of what would have been expected in the early morning (mean = 8.7 ± 6.1 individuals, range 1–19; $\text{mean}_{\text{lick use}} = 87.5 \pm 72.5$ bird min, $n = 7$ afternoons; $\text{mean}_{\text{lick use all mornings}} = 2,540 \pm 2,365$ bird min, $n = 606$ mornings).

Lick use the day before did not show the predicted negative correlation with lick use for all taxa combined (Table 2). When analyzed independently, five taxa showed significant positive correlations between lick use on consecutive days (all $P < 0.05$; Table 3). Similarly, the number of days since the lick was used did not show the predicted positive correlation with lick use (Table 2), and when taxa were analyzed separately, four species showed negative correlations between these variables (all $P < 0.05$; Table 3).

DISCUSSION

Twenty-eight species were seen eating clay at this site, making it the most species-rich avian geophagy site documented (Diamond et al. 1999, Burger and Gochfeld 2003, Brightsmith and Aramburú in press). As with other sites, parrots dominated and pigeons and Galliformes were observed regularly. As hypothesized, inclement weather (morning rain, overnight rain, and morning fog) reduced avian lick use. Lick use varied seasonally but did not vary among years. I did not find the hypothesized increase in lick use following days of low bird use or periods of inclement weather.

of the observations and significantly reduced total lick use. Reasons why birds use the lick less in fog are unknown but could be due to difficulties in navigation, increased chance of collision during flight, or increased probability of predation (Pyle et al. 1993, Bevanger 1994). Parrots using this site come from at least 16 km (DJB unpubl. data) and navigation over such distances could be more difficult or dangerous in foggy conditions. In general, animals approaching geophagy sites are very wary (Izawa 1993, Burger and Gochfeld 2003) presumably due to increased predator densities in the vicinity of geophagy sites (Klaus and Schmid 1998). This wariness is evident at the Tambopata lick and may contribute to the low rate of predation recorded during our work ($n = 4$ confirmed kills in 4,282 hr of observation [DJB unpubl. data], in an area with 34 species of raptors [Rainforest Expeditions 2001]). Birds may be more wary or unwilling to go to the lick during fog if fog reduces their ability to detect approaching predators. The significant interaction between fog and month found for Mealy Parrots suggests that the negative effect of fog varies depending on the month. This could be due to seasonal variation in the density of fog or variation in Mealy Parrots' responses to fog.

Weather index had a strong effect on total lick use. The birds used the lick much less on rainy mornings and more on sunny mornings. While correlations do not prove causality, my observations indicate that birds did not arrive in the area of the lick on rainy mornings, and they frequently abandoned not just the lick itself, but the entire area around the lick as storms approached or as rain began. These observations suggest that rain directly reduced the use of the lick. It is conceivable that the reduction in lick use was due to the birds not wanting to perch on or eat wet soil; the finding that lick use was less on mornings after overnight rain provides some support for this. However, the clays the birds prefer are waterproof due to the high clay and sodium contents (Tan 1996, Gilardi et al. 1999, Brightsmith and Aramburú in press). Water does not penetrate these soils and should have little or no effect on their chemical composition. The finding that lick use on rainy mornings was reduced is consistent with other studies that have shown general reductions in bird activity

Weather effects.—Fog occurred during 20%

during inclement weather (Beintema 1989, Keast 1994, Lengagne and Slater 2002).

Observers in Tambopata have long believed that total lick use is less during the cold weather associated with polar cold snaps or *frijas*. Such cold weather is known to reduce the level of bird activity in warm tropical climates (McClure 1975, Barry and Chorley 1998). My analysis does not support this contention, but it should be noted that the present data set contained only 13 mornings of bird data during *frijas*. Red-and-green Macaws and Orange-cheeked Parrots did show the expected decreased lick use with decreased minimum temperature, suggesting that they may reduce lick use during colder mornings.

When analyzed separately, 9 of 12 species showed reductions in lick use due to inclement weather. Reasons for the variation among taxa are not known and there are no clear inter-specific patterns that suggest an explanation. The parrot species studied here are thought to eat soil for sodium and protection from dietary toxins (Gilardi et al. 1999, Brightsmith and Aramburú in press). Unfortunately, our understanding of the ecological importance of geophagy at this time is insufficient to extrapolate the ecological consequences of this reduction in clay consumption. However, if climate change alters the timing, distribution, or quantity of rainfall, it could have unexpected consequences for these geophagous species.

Seasonal and annual effects.—Geophagy is highly seasonal for nearly all species studied, and the birds at Tambopata are no exception (March and Sadleir 1975, Jones and Hanson 1985, Sanders 1999, Keppie and Braun 2000). For most species, seasonal changes in geophagy are closely linked to diet changes or reproduction (Jones and Hanson 1985, Smedley and Eisner 1996, Sanders 1999). This appears to be the case in Tambopata, as well, where parrots show a sharp increase in lick use during breeding (DJB unpubl. data).

Overall lick use did not vary significantly among years, despite the fact that floods, landslides, and the natural change in the river course have altered the face of the lick during the course of this study. For Red-and-green and Blue-and-yellow macaws, the total amount of lick use in the mornings increased significantly as the study progressed. This is

probably not ecologically significant, as these birds use the lick much more during the late morning and afternoons, outside the time periods considered in these analyses (Burger and Gochfeld 2003, DJB unpubl. data). Yellow-crowned Parrots and White-eyed Parakeets showed significant declines during the course of the study; the reasons for these declines are unknown. There were no significant anthropogenic habitat changes near the study site. Both species are predominantly associated with successional habitats, but the Dusky-headed Parakeet (*Aratinga weddellii*) and Blue-headed Parrots (*Pionus menstruus*) that share these habitats show no similar declines (Forshaw 1989). There are at least two other major clay licks within 50 km of the Tambopata Research Center, and birds moving among these licks could cause the fluctuations. Alternatively, the declines may be part of natural population cycles.

Compensation for lick use lost to inclement weather.—On days when it rained during the early morning (before 07:30), >95% of the members of the nine “early morning” parrot species listed in Table 1 did not eat soil, even if the rest of the day was clear and sunny. Every day there were groups of large macaws that used the lick in the late morning and afternoon (DJB unpubl. data). As a result, large numbers of parrots that were rained out in the morning could have joined these macaw groups and used the lick later in the day. Instead, only a few birds occasionally joined these groups. Effects of weather are strongest on behaviors that are not essential for immediate survival, such as singing, migrating, communal roosting, and flying (Pyle et al. 1993, Keast 1994, Cougill and Marsden 2004). In comparison, either foraging is not as strongly suppressed by inclement weather (Stinson et al. 1987) or lost foraging opportunities are made up through increased effort after the weather clears (Durell et al. 2001). The strong effects of climate and the apparent lack of compensation when birds are denied access to soil suggest that birds do not suffer dire consequences if they are unable to eat soil for a few days, but more detailed studies are needed to test this hypothesis.

To date, there are no data on how often individual birds eat clay. An anecdotal account in Munn (1992) suggests that Red-and-green

Macaws in Manu come to the lick once every 2 to 3 days. If this were the case for the early morning species at Tambopata, I should have found greater lick use on days after the lick was not used, or that lick use was negatively related to lick use the previous day. However, I found that lick use was not correlated with lick use on the previous day. This suggests that the birds make daily decisions to visit the lick based on weather and season and not the amount of time since they have last eaten clay. It also suggests that the birds do not consume more clay to compensate for missed days. For five taxa, the number of birds the day before was positively correlated with lick use, and for four of these taxa the number of days since they had used the lick was negatively associated with lick use. The five species involved (two large macaws, White-bellied Parrot, White-eyed Parakeet, and Blue-throated Piping-Guan) span the range of habitat preference, body size, abundance, group size, seasonality of lick use, and time of day of lick use, making interpretation of this finding difficult.

Reasons for soil consumption.—Previous studies suggest that birds in southeastern Peru consume soil for protection from dietary toxins, sodium deficiency, or both, and the findings of this study may provide some insight (Diamond et al. 1999, Gilardi et al. 1999, Brightsmith and Aramburú in press). The soil protects the birds from toxins by direct adsorption, stimulation of the gut to produce more mucus, and formation of a physical barrier between toxic foods and the gut lining (Gilardi et al. 1999). In addition, sodium and other minerals in the soil may protect the small intestine from tannins (Freeland et al. 1985). The soil stays in the digestive tract for approximately 12 hr; thus, protection from toxins requires daily ingestion of clay before foraging (Gilardi et al. 1999). Because protection from toxins is only effective over the short term, birds should not compensate for days when soil was not consumed. However, the effect of soil on sodium balance is likely to last over more than just 12 hr and birds could make up for missed days through increased consumption on fair weather days. In addition, the timing of clay consumption should be less important if sodium deficiency is driving lick use. As predicted by the pro-

tection from toxins hypothesis, most parrots ate clay first thing in the morning before going off to forage. In addition, birds did not compensate for missed days. These lines of evidence suggest that protection from toxins could be driving lick use. However, evidence from a nearby site suggests that these species choose soil based on its sodium content and not its ability to adsorb dietary toxins (Brightsmith and Aramburú in press). Further insight into lick use would be gained by studies that compare foraging behavior and toxicity of foods eaten on days when birds do and do not have access to clay, and by comparative studies of birds that use the lick in the early morning with those that use the lick later in the day.

The causes and consequences of geophagy are admittedly complex. Detailed physiological and geochemical studies have provided us with insights into the potential benefits of this behavior (Freeland et al. 1985, Jones and Hanson 1985, Gilardi et al. 1999, Mahaney et al. 1999). However, few studies have tied these results directly to the ecology and behavior of species in the wild. This study shows that inclement weather reduces lick use and that birds do not eat more soil to compensate for geophagy opportunities lost to inclement weather. These findings suggest that neutralization of toxins could be driving avian geophagy in this system, but investigators must continue to explore the complex temporal, seasonal, spatial, and taxonomic patterns in soil consumption if we are to determine its true ecological importance.

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